AN INTERESTING FEATURE IN THE VENATION OF HELICOPSYCHE, THE MOLANNIDAE, AND THE LEPTOCERIDAE.

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The conclusions recorded in a recent paper by Prof. Martynov* regarding the venation of the Trichopterous genus Helicopsyche lead me to anticipate here one of several somewhat revolutionary views on the venation of the Trichoptera to which I have come during the progress of work on a rather extended report on that order of insects.

For the sake of comparison a figure is here given of the venation of the fore wing of Rhyacophila (Fig. 1), representing an extremely primitive type. The homologies indicated in this figure are so simple as to require no comment except as regards the branches of subcosta (Sc) and of cubitus and the anals. None of these is here considered and attention is directed only to radius which in this genus appears in absolutely primitive condition, that is, with R_1 running free to the margin and with the radial sector (Rs) dichotomously branched. In very many Trichoptera there is a cross vein from R_3 to R_4 setting off what is called the discal cell. Near the base of cell R_4 (the cell bounded by R_4 and R_5) there is indicated a very small corneous point which is present in the vast majority of Trichopterous wings.

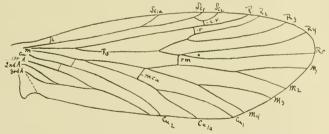


Fig. 1. Venation of fore wing of Rhyacophila sp.

Martynov reaches the conclusion that radius is also found in practically the typical condition in Helicopsyche (Fig. 2), that is, that cell R_4 in both fore and hind wings is not obliterated by the fusion of R_4 and R_5 as might at first sight appear to be the case.

^{*}Martynov, A. B. On two Collections of Trichoptera from Peru. Annuaire du Musee Zool. de l'Acad. Imperiale des Sci. de St. Petersburg. Vol. 17 (1912), 40 pp., Figs. 1-59.

That this view is correct seems to admit of no doubt. In the American species (*H. borealis* Hag.) the relations are entirely clear. R_5 leaves R_4 at nearly a right angle and then again turns sharply to the wing margin; the cross vein rm meets the vein at the latter angle, and is in a nearly horizontal position. One might therefore easily be deceived into thinking that the cross vein rm and the distal part of R_5 with which it is in direct line together constitute a branch of media. A failure to recognize the true relation has forced most authors to leave this vein unidentified in their figures. The exact position of the base of R_5 varies somewhat within the genus and also within the species;

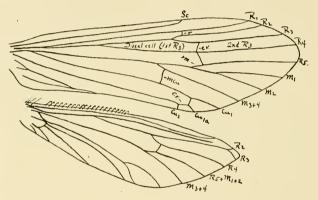


Fig. 2. Venation of Helicopsyche borealis.

in specimens of *H. borealis* (Fig. 2 and Fig. 3a) the cross vein rm is left intact though out of the usual position as already shown, in Martynov's figure (l. c., Fig. 2, copied in Fig. 3b) of *H. minuscula* the angle in R_5 just touches M_{1+2} so that the cross vein rm is obliterated and its function is assumed by the base of R_5 , in Ulmer's figure of *H. borealis* (Genera Insect. Fasc. 60, pl. 11, fig. 98, copied in Fig. 3c) the base of R_5 has migrated still farther back so as to be still more deceptive in its resemblance to the cross vein which it has displaced. Ulmer has recently described some related fossil genera in one of which (Palaeohelicopsyche*) the female has the cross vein rm present while it has been displaced in the male.

^{*}Ulmer, Georg. Die Trichopteren des baltischen Bernsteins. Schriften der physikalisch-ökonomischen Ges. zu Königsberg. Beiträge zur Naturkunde Preussens. Heft 10 (1912), p. 308.

1913] Helicopsyche Molannidæ and Leptoceridæ

Attention has already been called to the small corneous point that occurs in the base of cell R_4 in almost all Trichoptera. Perhaps the position of this point may be given some weight in the determination of the veins between which it occurs, as is done in the discussion of the venation of the Molannidæ and the Leptoceridæ given later in this paper. In the case of Helicopsyche the evidence from this source now available is incomplete and apparently contradictory. In Ulmer's figure of the closely related genus Tetanonema (Genera Insect. Fasc. 60, pl. 12, fig. 100) the corneous point appears in its normal position in cell R_4 but in his figure of *H. sperata* (l. c., pl. 11, fig. 97) and in the figures of several related genera

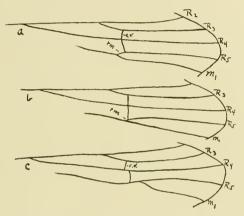


Fig. 3. a, Radius of the fore wing of Helicopsyche borealis. b, The same from H. minuscula (after Martynov). c, Another specimen of H. borealis (after Ulmer).

described in his fine work on the fossil forms it is found in cell 2nd R_3 , that is, in the cell immediately anterior to the one in which it normally occurs. On the other hand this spot is not shown in McLachlan's figures of *H. sperata* and *H. borealis*, Martynov does not find it in *H. sperata* and the study of a large series of *H. borealis* fails to reveal a single occurrence. Since Ulmer's observations are on material in amber there may be greater chance for error though it seems unlikely that this should happen in several cases. At any rate, Tetanonema and Saetotricha, the only closely related modern forms, should be re-examined in this connection. If Ulmer's figures are correct these cases form the only exception to the rule that the corneous point occurs, if it occurs at all, in the base of cell R_4 . In some groups there is a similar spot in the distal part of cell M of the fore wing (Fig. 8). This spot which has apparently been but little noted, while it is characteristic of fewer groups of Trichoptera is as constant in position as are those of cell R_4 in the fore and hind wings.

On account of the reduced number of segments in the male palpus Helicopsyche has always been placed in the very heterogeneous family Sericostomatidæ though its isolated position within that family has been fully recognized. Its venation, as interpreted by Martynov, has some resemblance in the points here considered to the very abnormal venation of the Molannidæ and to that of the Leptoceridæ.

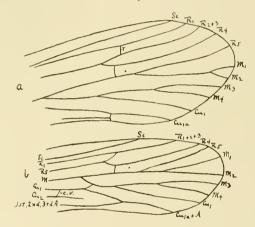


Fig. 4. *a*, Apical part of fore wing of Molannodes zelleri. *b*, Same of Molanna cinerea \mathfrak{Q} .

In the Molannidæ there has come about a very considerable shifting in the position of the veins as a result doubtless of the unusual position of the wings—these being rolled more or less about the body. In the European genus Molannodes (Fig. 4a) the condition with respect to radius is strikingly like that which is at least sometimes found in Helicopsyche (Fig. 3c), that is, R_5 has arched back into M_{1+2} obliterating the cross vein rm and leaving its own base in the regular position of that cross vein. There is a further reduction in the fusion of R_2 and R_3 . In Molanna cinerea (Fig. 4b) there is a similar condition but R_{2+3} has also fused with R_1 . In both genera M_{3+4} has migrated upon Cu_1 just as R_5 has upon M_{1+2} . Radius of the hind wing may be similarly interpreted. While the limits of this paper preclude discussion of the other modifications, enough has been indicated to show that the determination of the homologies in the venation of the Molannidæ and the Beraeinæ need not be given up in despair.

While in the case of the Molannidæ the suggestions here made may help to bring order out of what has admittedly been chaos, it may seem that in extending the same interpretation to the Leptoceridæ the reverse is true. In this latter family there has been uncertainty as to the homology of the veins but the entire family is practically homogeneous in this respect and everyone seems to have been satisfied to recognize equivalents within these limits without determining the larger relations. Thus McLachlan (Rev. and Syn. p. 282) states that the application of the notation in this family (his section 3) is "not very satisfactory" and he leaves the veins and cells between R₃ and Cu, unidentified except in the genus Triaenodes and in the females of Leptocerus. In these latter cases there is apparently an evident recurrence of the 2nd and 3rd cells (cells R₄ and M₁) respectively, but as will be indicated further on this appearance may be illusory. Later authors have followed McLachlan's practice and no suggestion has so far been made as to the manner by which the evident reduction of the venation of the Leptoceridæ has come about.

The venation of a species of Leptocerus (Fig. 5) may serve as typical for the family. Attention is directed to radius of the fore wing which is similar in appearance in practically all members of the family and which apparently differs from the typical 5-branched radius only in having R_4 and R_5 fused. The only reason for questioning this interpretation is found in the fact that the corneous point then falls behind instead of in front of R_5 . Exactly comparable conditions are found in the hind wing (Fig. 5b). It may possibly not be justifiable to discard the obvious interpretation of these veins because of the location of a minute structure whose significance is wholly unknown and whose position may therefore depend upon factors which have nothing whatever to do with the venation. It is, however, a most remarkable fact that while these points are absent in a few groups, they are never found outside of their respective cells no matter what curious modifications these cells undergo. In fact a condition like that shown in Fig. 6 (Smicridea sp.) suggests that the corneous point submits to annihilation in preference to displacement.

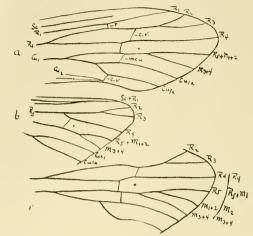


Fig. 5. *a*, Apical venation of fore wing of Leptocerus sp. σ^{2} . *b*, Hind wing of same. *c*, Fore wing of female of same.

If then we give any weight to the comparison with Helicopsyche and the Molannidæ and to the position of the corneous points we should conclude that in the Leptoceridæ also R_5 has arched into M_{1+2} its distal end fusing with the latter compound vein and that what appears to be the cross vein rm is in reality the base of R_5 .



Fig. 6. Radial sector in the fore wing of Smicridea divisa.

In almost all of the Leptoceridæ media is reduced to two branches but in the subfamily Triplectidinæ and in females of the genus Leptocerus a more generalized condition obtains, that is, media is apparently three branched (Fig. 5c). If the view here advocated is correct these generalized Leptoceridæ are in exactly the same condition as regards the relation of R_5 and media as is Helicopsyche, that is, R_5 has arched into M_{1+2} but has not fused with it distally. There is of course the other possibility that it is M_1 and M_2 that are separate and R_5 and M_1 that have fused. The alternative interpretations are indicated in Fig. 5c. To decide between these possibilities we should have to find out which fusion took place earlier in the phylogenetic series and on this question the evidence seems inconclusive.

While the purpose of this paper is fulfilled in showing that the modifications of radius may be similarly interpreted in Helicopsyche, the Molannidæ, and the Leptoceridæ, another instance of similar modifications may be added lest the basal shifting of a distal branch from one main stem to another should seem unlikely in this order. A parallel case is shown in media of the fore wing of Oecetis^{*}. Authors from McLachlan

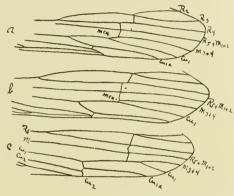


Fig. 7. Venation of apical part of fore wing of species of Occetia. *a*, Occetia fumosa. *b*, Occetia incerta. *c*, Occetia testacea (after McLachlan).

on agree in saying that media in Oecetis is absolutely simple or unbranched. No one seems to have been disturbed by the fact that on such an interpretation an extra branch would have to be assigned to cubitus. As a matter of fact media is always two branched in Oecetis as it is in most of the other Leptoceridæ. In O. fumosa (Fig. 7a) while there is slight variation in exact position, M_{3+4} leaves M_{1+2} at about right angles; it bends sharply and then proceeds to the wing margin. At the latter angle it is joined by the cross vein m-cu which is in line with the distal end of M_{3+4} so that the resulting deceptive appearance is that of an extra branch on the anterior side of cubitus joined to media by a cross vein which is in reality the base of M_{3+4} . In O. incerta (Fig. 7b) the cross vein m-cu is very short, in some

^{*}I include here Oecetina Banks and Oecetodes Ulmer.

specimens it is wholly lacking. Finally in such forms as the European *O. testacea* (Fig. 7c) the base of M_{3+4} has migrated farther back on Cu₁ and in this position its true nature as a part of M_{3+4} is far from obvious. In such a case the vein becomes virtually a cross vein and migrates according to the mechanical stress in flight without reference to the distal part of the vein which is left stranded with a new basal connection. Other instances of this sort occur in the Trichoptera and they are not uncommon in other orders.

The facts here presented may be of some significance in their bearing on the question of the systematic position of the Helicopsychinæ. This subfamily has always been placed in the Sericostomatidæ because of the unequal number of segments in the palpi of the male and female, though it has always been clearly recognized that it bears no close relationship to any of the heterogeneous groups included in that family. Thienemann, Ulmer, and Martynov have each suggested that a new subfamily should be erected for the genera Helicopsyche, Tetanonema, and Saetotricha, and Ulmer and Martynov have during the past year almost simultaneously described the subfamily Helicopsychinæ, Ulmer's description being slightly the earlier.

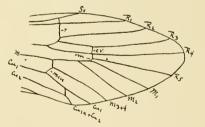


Fig. 8. Venation of apical part of fore wing of Sericostoma sp.

In his recent work on the fossil forms Ulmer lists the Helicopsychinæ among the Sericostomatidæ but in this work (p.376) he makes the first suggestion that these forms may possibly show affinities to the Leptoceridæ though he gives, so far as I can find, no reason for the statement. What has been given above certainly confirms the impression which Ulmer has stated since in the Helicopsychinæ, the Molannidæ, and the Leptoceridæ, R_5 shows an increasing tendency to migrate upon M_{1+2} —a condition not seen elsewhere in the Trichoptera, though the sharp angle in R_5 seen in Sericostoma (Fig. 8) and other forms might be regarded as a beginning of that tendency. It is interesting to note that there are some other characters not found in the Sericostomatidæ which Helicopsyche shares with genera of other familes. Thus it has the costal hooks on the hind wings which are found well developed only in the Leptoceridæ, Molannidæ, and the Macronematinæ (Hydropsychidæ). I find also that *II. borealis* has the peculiar fenestrated terga in the posterior abdominal segments heretofore found only in certain species of Oecetis—a genus of Leptoceridæ.

Taken altogether the facts presented do not do more than emphasize the isolated position of the Helicopsychinæ and suggest that this subfamily may be regarded as an early offshoot from the Leptocerid stem which in the condition of the palpi has diverged from the typical form in the same way as have the Sericostomatidæ.